

WHITE PINE BLISTER RUST RESISTANCE
MECHANISMS OF SUGAR AND WESTERN WHITE
PINES USED IN REGION 6

by
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A. Introduction

White pine blister rust caused by *Cronartium ribicola* has been a major forest disease in North America since its introduction at the turn of this century. Its devastating effect on important forest tree species prompted many agencies to initiate control programs such as eradication of ribes and others that have been tried and discarded. The USDA Forest Service Region 6 program for breeding of western white pine and sugar pine resistant to blister rust has been in existence since 1955. Through the years candidate trees were selected and seedlings from these trees tested for resistance to white pine blister rust. Some of the resistance factors provide us with long lasting, uniform resistance. Others provide only short term resistance against specific races of the rust. The first are referred to as horizontal and the second as vertical resistance mechanisms (Figure 1).



Figure 1. Graphical comparison between vertical and horizontal types of resistance.

Vertical resistance types are most often controlled by few genes that produce large effects (major genes), and differences are usually qualitative. Vertical resistance in the host can be "lost" if the rust changes and overcomes resistance (Vanderplank 1978).

Horizontal resistance or uniform resistance is most often inherited by polygenes, and differences are usually quantitative (Hoff 1979, Vanderplank 1978). This type of resistance is more stable and is not "lost" to a change in the pathogen but can be reduced when virulence in the pathogen population increases.

The rust inoculum used at Dorena comes from several different sources around the Region and from several ribes species. It is distributed as uniformly as practical for each source and ribes species in the inoculation chamber so that each seedling will have a nearly equal chance of being exposed to the various races of the rust. In addition inoculum loads are closely monitored to obtain a rust spore cast most suitable for exposing the composite of resistance reactions selected for in the resistance screening process. The planting design allows statistical adjustments based on the spore load actually obtained.

Using the example in Figure 1 for vertical resistance it is evident that many seedlings exposed to races 1 and 2 would be resistant but the same seedlings exposed to races 3 and 5 would not be resistant. Therefore, with the mixture of rust races and inoculum load used at Dorena many seedlings will have partial resistance reactions for the vertical resistance mechanisms. Using early shed of infected secondary needles as an example, needles infected only

with race 1 would be shed while those infected with race 3 would not. Seedlings having complete early shed of infected needles and those with high but incomplete early shed of infected needles are suitable selections for this resistance mechanism.

B. Other Pertinent Region 6 Tree Improvement Papers

Most Region 6 Tree Improvement Papers apply to some extent to the white pine blister rust resistant sugar and western white pine program. The following papers are especially significant:

<u>Title</u>	<u>Paper Number</u>
Selection of White Pine for White Pine Blister Rust Resistance Screening	5
Development of Western White Pine and Sugar Pine Seed Production Areas	6
Seed Orchard Development	7
Selection of Seed Orchard Sites	9
Pollen Management in Seed Orchards	25
Scion Collection, Handling, Grafting, and Graft Protection	28
Some Genetic Considerations in the Maintenance and Enhancement of Balance in Host-Pest Systems	37
Breeding Zone Statistics for the Pacific Northwest Region	38
Advanced Generation Breeding	44
Abortion of Reproduction Organs in Pacific Northwest Conifers	48
Background Paper on Developing, Breeding, and Deploying White Pine Blister Rust Resistant Sugar Pine and Western White Pine in the Pacific Northwest Region	50
Charter for and Mission of Dorena Tree Improvement Center	51
Selection of White Pines for Production Seed Harvest, Seed Orchards, and Breeding Arboreetums Based on White Pine Blister Rust Screening at Dorena Tree Improvement Center	53

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C. Program Goal

The program goal is to develop multifactor resistant lines of sugar and western white pines to white pine blister rust as shown in table 1 and to introduce these lines into seed orchards for the production of forestation seed.

These multifactor lines make maximum use of horizontal resistance mechanisms. They use selected vertical resistance mechanisms to maintain a balance between the various races of white pine blister rust to avoid directional selection for a race of the rust that can overcome all the vertical resistance used, and reduce the effectiveness of the horizontal resistance. This is an idealized goal which will not be attained in the near future. The four lines are to be as equally represented as possible but randomly distributed in a seed orchard. The first generation seed orchards shall have at least level 1 and 2 resistance with as much level 3 and 4 resistance and tolerance as is available. Subsequent generation seed orchards will come closer and closer to the idealized goal. The goal also sets the direction for the breeding program to increase resistance, refer to R-6 Tree Improvement Paper No. 44 for specific details.

Table 1. The Multifactor Lines.

Level and Type of Resistance	Line			
	1	2	3	4
1 Horizontal	Reduced needle lesion frequency in secondary needles	Reduced Needle lesion frequency in secondary needles	Reduced Needle lesion frequency in secondary needles	Reduced Needle lesion frequency in secondary needles
2 Vertical	No spot formation in secondary needles	Early shed of infected secondary needles	short shoot reaction	Bark reactions
3 Horizontal	Slow fungus growth in secondary needles	slow fungus growth in secondary needles	slow fungus growth in secondary needles	Slow fungus growth in secondary needles
4 Horizontal	Slow canker growth	Slow canker growth	Slow canker growth	Slow canker growth
5 Tolerance	Tolerance in stem	Tolerance in stem	Tolerance in stem	Tolerance in stem

The plant parts involved in infection by blister rust are shown in Figure 2. No selection is made against other resistance mechanisms when selecting for the eight resistance mechanisms used in the multifactor lines, therefore these other resistance mechanisms should not be eliminated from the lines, this provides further stability to the lines.

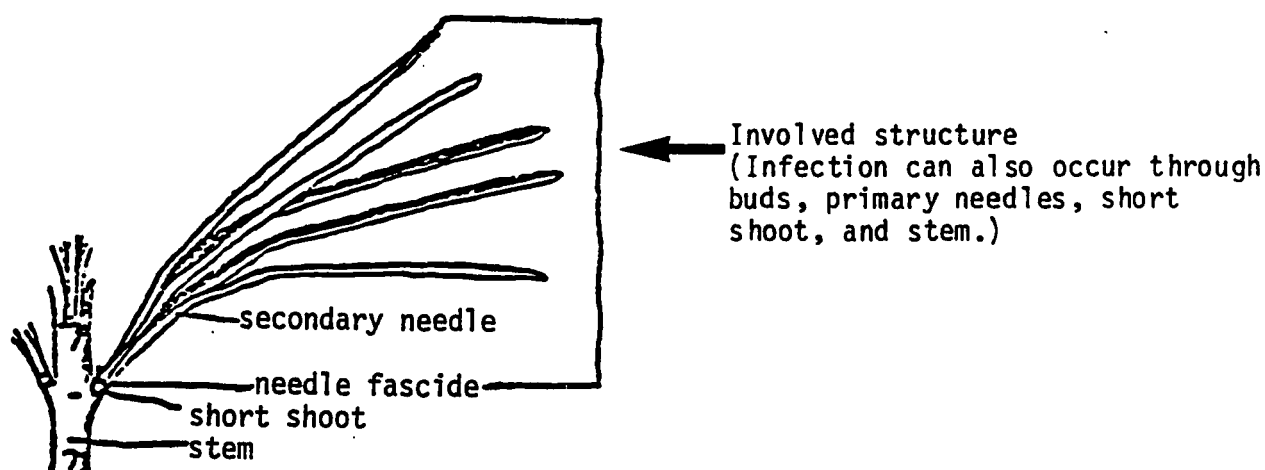


Figure 2. Structures involved in the infection of secondary needles by Cronartium ribicola.

D. Description of Resistance Mechanisms and Tolerance

The following is a description of each of the resistance mechanisms and tolerance that are utilized in the R-6 breeding program:

1. Reduced needle lesion frequency in secondary needles. This factor is a horizontal resistance mechanism. Breeding for reduction of spot frequency is difficult because the number of rust spores per square centimeter must be controlled during artificial inoculation and needle spot frequencies must be scored after inoculation in order to detect it. It is mainly controlled by a single gene. Seedlings with this resistance have significantly less blister rust spots on secondary needles than susceptible seedlings.

2. No spot formation in secondary needles. No needle spots form on secondary needles after inoculation. This is considered a threshold character with its expression dependent upon inoculum load. Genetic control of this vertical resistance mechanism has not been determined (Hoff and McDonald, 1980).

Since this is a vertical resistance mechanism, some races of the rust included in the inoculum may by-pass this resistance and cause needle spots. When this resistance is by-passed by a rust race at low frequency in the inoculum, this resistance may be inseparable from reduced needle lesion frequency in secondary needles resistance.

3. Premature shedding of infected secondary needles. The infected needles drop off before the fungus can enter the short shoot and is thus prevented from entering the stem. Seedlings with this trait remain healthy when secondary needle shed is complete and no blister rust infections occurred through primary needles or by bypassing the needles. This mechanism is vertical and is considered to have simple recessive gene inheritance. (Hoff et. al., 1976).

Since this is a vertical resistance mechanism, some races of the rust included in the inoculum may by-pass this resistance and cause cankers. When this occurs, this resistance is not exposed for selection.

4. Fungicidal reaction in the short shoot. The resistance reaction is initiated by the interaction of the fungus with the plant tissue in the short shoot and results in the death of the fungus. This mechanism when complete for all rust races attacking a seedling prevents the rust from entering the stem and the seedling remains healthy provided that no blister rust infections occurred through primary needles or by bypassing the needles. This resistance mechanism is also vertical and is considered to have simple recessive gene inheritance (Hoff and McDonald, 1971).

This is a vertical resistance mechanism, therefore some races of the rust included in the inoculum may by-pass this resistance and cause cankers. When this occurs, this resistance is not exposed for selection.

5. Bark reaction. This mechanism is a result of the interaction of the fungus and the stem tissue which results in a dead canker. This resistance mechanism is vertical and is inherited by several genes (oligogenic) (Bingham et. al., 1960/Hoff and McDonald, 1972). It must be measured before pycnia are formed on the blister rust canker or shortly thereafter to avoid confounding it with the action of other fungi that infect blister rust affected tissue and cause canker mortality.

Since this is a vertical resistance mechanism, some races of the rust included in the inoculum may by-pass this resistance, produce normal cankers, and cause tree mortality. When this occurs, a tree will have both normal and reaction cankers.

6. Slow fungus growth in secondary needles. This resistance mechanism slows down the growth of the fungus in secondary needles and thus increases the time between needle infection and stem infection. It is a horizontal resistance mechanism with high heritability and polygene control (Hoff and McDonald, 1980).

7. Slow canker growth. A typical blister rust canker occurs on the stem. The canker does not girdle the tree as rapidly as a normally growing canker. It is a horizontal mechanism controlled by many genes (polygenes).

8. Tolerance. This is a plant-disease organism relationship which can be of the following two types.

(1) Symbiosis. The plant and the organism capable of causing disease derive equal benefit from the association.

(2) Parasitism. The plant derives no benefit from the association while the disease organism does. The plant does not sustain serious economic damage.

E. Scoring Procedures For Resistance and Tolerance During Rust Screening

1. Introduction - The following resistance mechanisms are associated with secondary needles:

- a. Reduced needle lesion frequency in secondary needles.
- b. No spot formation in secondary needles.
- c. Premature shedding of infected secondary needles.
- d. Fungicidal reaction in short shoot.
- e. Slow fungus growth in secondary needles.

Scoring for these resistance mechanisms is based on secondary needles in the portion of the seedling stem which had first year secondary needles at the time of inoculation with white pine blister rust. All of these resistance mechanisms may be by-passed by infection through buds, primary needles, short shoot, or the stem. When the vertical resistance mechanisms are by-passed, later occurring resistance mechanisms are exposed for selection.

The following resistance mechanisms are associated with the bark and cambium:

- a. Bark reaction
- b. Slow canker growth
- c. Tolerance

These resistance mechanisms are not by-passed by infection through buds, primary needles, short shoot, or the stem.

2. Inspection Schedule - Table 2 shows the inspection schedule and the type of data collected in the white pine blister rust resistance screening at the Dorena Tree Improvement Center.

Table 2. Resistance Inspection Schedule.

Inspection	Date of Inspection	Data Collection and Resistance Mechanisms
First Inspection	Spring following previous fall inoculation	Needle lesion frequency in secondary needles Mortality
Second Inspection	Fall one year after inoculation	Needle spots on second year secondary needles Canker location Canker type Mortality
Third Inspection	Late summer-fall two years after inoculation	Canker location Canker type Mortality
Fourth Inspection	Late summer-fall three years after inoculation	Canker type for trees with slow fungus growth in secondary needles Mortality
Fifth Inspection	Fall four years after inoculation	Live canker data Tree growth Mortality
Sixth Inspection	Fall five years after inoculation	Same as fifth inspection

3. Resistance Scoring - Resistance scoring during rust screening is based upon rust development. The optimum time for scoring may vary somewhat from year-to-year due to environmental conditions that affect rust development. The normal schedule for resistance scoring during rust screening at the Dorena Tree Improvement Center is as follows. Refer to table 3 for a normal time line comparison for the identification of the various resistance mechanisms.

(1) Reduced needle lesion frequency in secondary needles. Seedlings with this resistance are identified based on the performance of the calibration family included in each run. The number of needle spots per unit length of second year secondary needles on each seedling in the calibration family is determined. Each tree in the calibration family is assigned to one of five needle spot classes. One class is zero, the other classes are determined by dividing the range in spots per seedling based on a uniform unit of needle length into four classes. Classes are numbered consecutively 0, 1, 2, 3, and 4 with 0 having no spots and 4 the most spots on second year secondary needles. Seedlings in category 1 are considered to have reduced needle lesion frequency in secondary needle resistance.

(2) No spot formation in secondary needles. - Seedlings with this resistance, when the resistance is complete, are in needle spot class zero.

(3) Premature shedding of infected secondary needles. Seedlings with this resistance, when the resistance is complete, have needle spots on second year secondary needles the spring following inoculation, lack needle spots on second year secondary needles the following fall, and are free of blister rust stem infection in the stem area of third year secondary needles two years after inoculation and this stem area remains free of blister rust infection..

(4) Fungicidal reaction in the short shoot. Seedlings with this resistance, when the resistance is complete, have needle spots on second year secondary needles the spring following inoculation, have needle spots on second year secondary needles the following fall, and are free of blister rust stem infection in the stem area of the third year secondary needles two years after inoculation and this stem area remains free of blister rust infection.

(5) Bark reaction. Seedlings with this resistance, when the resistance is complete, have 100 percent reaction cankers. When the resistance is incomplete, by-passed by a particular race of the rust, both normal and reaction cankers will be present on a seedling. A reaction canker is a dead canker with one of the typical bark reactions associated with this resistance.

Bark reaction scoring is most effective before pycnia are produced on the blister rust canker. When done later in the life cycle of white pine blister rust, bark reactions may be confounded by fungi such as the purple mold fungus (Tuberculina maxima) which kill blister rust infected stem and branch tissue.

Initial infection by the purple mold fungus takes place through pycnia and aecia. After infection, the purple mold fungus suppresses production of pycnia and aecia and inhibits growth and development of cankers (Wicker 1981). The aggressive race of the purple mold fungus present at the Dorena Tree Improvement Center usually completely kills blister rust cankers the spring following canker infection.

(6) Slow fungus growth in secondary needles. Seedlings with this resistance, when it is exposed, have needle spots on second year secondary needles in the fall the year after inoculation, lack evidence of blister rust stem infection in the stem area of the third year secondary needles two years after inoculation but subsequently have blister rust stem infection in this area.

(7) Slow canker growth. Seedlings with this resistance, when it is exposed, which do not have slow fungus growth in secondary needles die one year later than cankered seedlings without this resistance or are stunted. Seedlings which have slow fungus growth in secondary needles die two years later than cankered seedlings without this resistance or are stunted. This resistance is not completely seperable from tolerance. It may also be confused with slow canker growth caused by the purple mold fungus. Despite this possible confounding, stem infected seedlings which have delayed mortality or are stunted and surviving four or five years after inoculation with live basal stem cankers are considered to have this resistance.

(8) Tolerance. Normally growing seedlings with live basal stem cankers in the fall five years after inoculation are considered to have tolerance.

4. Data Collection

First Inspection

1. Needle spot categories - second year secondary needles.
0, 1, 2, 3, 4
2. Mortality
9 Dead tree. (Remove and include all seedlings without second year secondary needles in the dead tree class.)

Second Inspection

1. Needle Spots - second year secondary needles.
0 Absent
1 Present
2. Canker Location
0 No canker.
1 Canker on second year secondary needle portion of stem.
2 Canker on other than second year secondary needle portion of stem.
3 Both 1 and 2.
3. Canker Type

<u>Normal Canker</u>	<u>Reaction Canker (Dead)</u>
0 Absent	0 Absent
1 Present	1 Present
4. Mortality
9 Dead tree

Third Inspection

1. Canker Location
0 No canker.
1 Canker on third year secondary needle portion of stem.
2 Canker on other than third year secondary needle portion of stem.
3 Both 1 and 2.
2. Canker Type (Bark reaction)
 - a. Normal canker
0 Absent
1 Present
 - b. Reaction canker (Dead)
0 Absent
1 Present
3. Mortality
9 Dead tree

Fourth Insepection

1. Canker Type
 - a. Normal canker
 - 0 Absent
 - 1 Present
 - b. Reaction canker (Dead)
 - 0 Absent
 - 1 Present
2. Mortality
 - 9 Dead tree

Fifth Inspection

1. Live basal stem canker
 - 0 Absent
 - 1 Present
2. Tree growth
 - 1 Normal
 - 2 Stunted
3. Mortality
 - 9 Dead tree

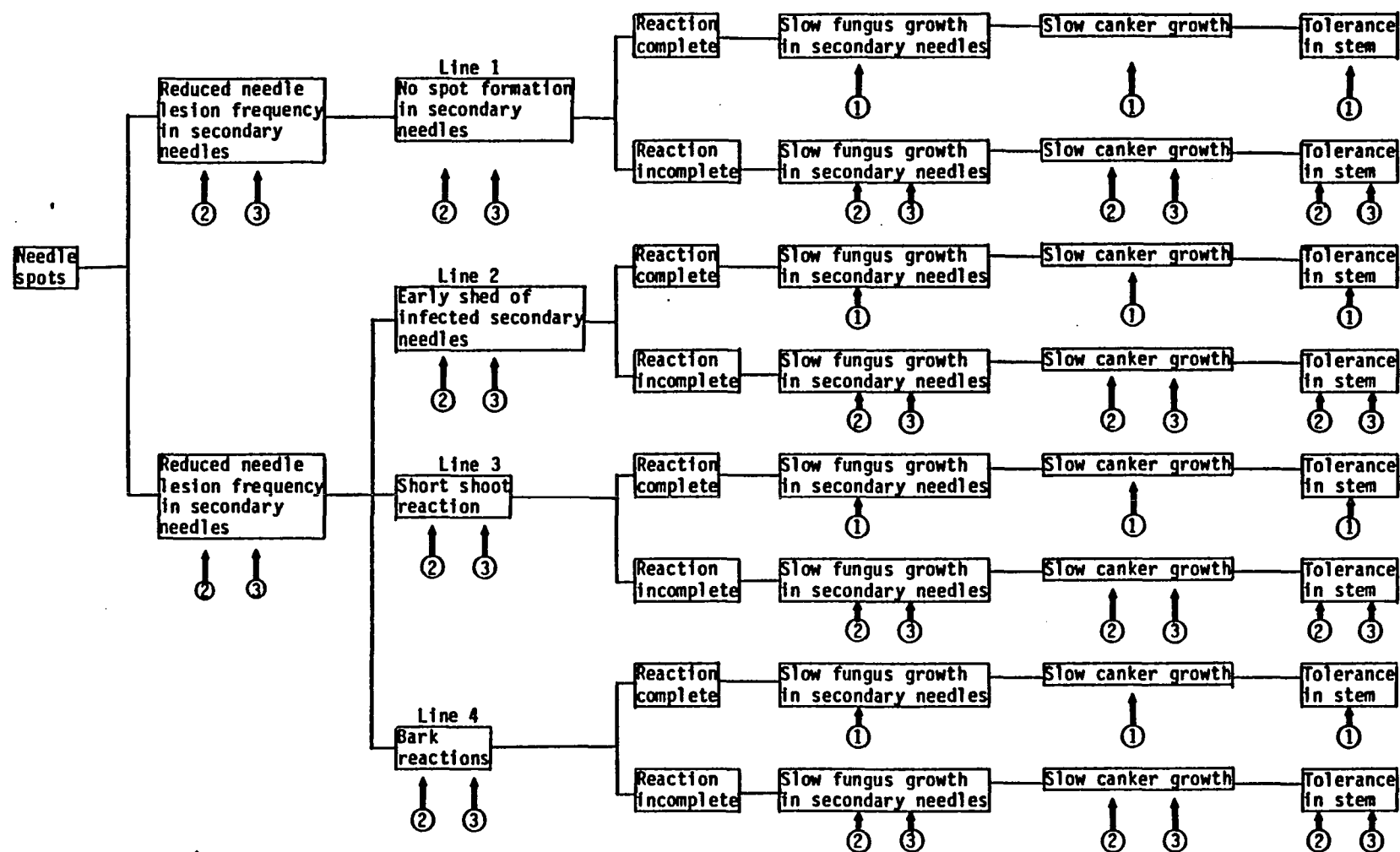
Sixth Inspection

1. Live basal stem canker
 - 0 Absent
 - 1 Present
2. Tree Growth
 - 1 Normal
 - 2 Stunted
3. Mortality
 - 9 Dead tree

F. Sequence of Selection and Type of Selection in Rust Resistance Screening at Dorena

The sequence and type of selection is displayed in table 4. A vertical resistance mechanism is complete when it is not by-passed by a particular race of the rust, or by bud, primary needle, short shoot, or direct stem infection by the rust. Refer to Region 6 Tree Improvement Paper 53 for assignment of trees to multifactor lines, seed orchards, and breeding arboretums.

Table 4. Sequence of Selection and Type of Selection*



Type of selection 

1. Family
2. Family and within family**
3. Individual***

* The sequence of selection applies to the selection process only. It does not imply that the various resistance mechanisms are dependent upon one another for occurrence or that they are controlled by the same alleles or genes.

** Family and within family selection in open pollinated families when resistance is from female parent and in controlled crosses.

*** Individual tree selection in open pollinated families when resistance is from male parent.

G. Preservation of Desirable Genotypes in the Rust Screening Test

Individual seedlings in the rust screening program at the Dorena Tree Improvement Center which have desirable resistance mechanisms shall be preserved for placement in seed orchards or breeding arboretums. Selected individuals may have to be preserved by grafting prior to the completion of the rust screening test. In most cases, it will always be better to preserve resistant seedlings which meet Region 6 criteria for placement in seed orchards and breeding arboretums than to go back to the parents. This means that only in rare instances shall parent trees be preserved in seed orchards or breeding arboretums for advanced generation breeding.

Table 5 shows the sequence for preserving desirable genotypes in the rust screening test.

H. Time Line For Activities After Seed is Available From Rust Resistant Candidate Trees

The time line for activities at the Dorena Tree Improvement Center and for Forests after seed is available from rust resistant candidate trees is shown in table 6. This time line applies in cooperative programs with others but activities may be limited by the scope of the cooperative effort.

Table 6. Time Line For Activities, Dorena and Forests

Year	←-----Dorena Activity-----	Forest Activity-----→
1.	Sow seed.	a. Report families sown to Forests and those with insufficient germination and seed on inventory. a. Schedule seed collection from trees from which more seed is needed. b. Harvest needed seed if available.
2.	Inoculate seedlings with blister rust after second growing season.	a. Report families with insufficient base to Forest and those for which additional seed is needed. a. Schedule seed collection from trees for which additional seed is needed. b. Harvest additional seed if available.
3.	First and second inspection for resistance.	a. Report results to Forests. a. Select parent trees from Dorena report from which to harvest seed per recommendations in Table 5. b. Make arrangements for inclusion of material from Dorena in seed orchards and breeding arboretums. c. Harvest seed from selected trees.
4.	Third inspection for resistance.	a. Report cumulative results to date to Forests. a. Review assignment of parent trees for forestation seed harvest. b. Protect promising threatened material in rust screening program by grafting. b. Make arrangements for including new material from Dorena in seed orchards and breeding arboretums. c. Advise Forests of material coming for seed orchards and breeding arboretums next year. c. Harvest seed from selected trees.
5.	Fourth inspection for resistance.	a. Report cumulative results to date to Forests. a. Review assignment of parent trees for forestation seed harvest. b. Protect promising threatened material in rust screening program by grafting. b. Include material grafted at Dorena last year in seed orchard or breeding arboretums. c. Advise Forests of material coming for seed orchards and breeding arboretums next year. c. Make arrangements for including new material from Dorena in seed orchards and breeding arboretums. d. Allocate material grafted previous year to Forests for seed orchards and breeding arboretums. d. Harvest seed from selected trees.
6.	Fifth inspection for resistance.	Repeat 5a, b, c, and d.
7.	Sixth inspection for resistance.	Repeat 5a, b, c, and d.

I. Recommended Use of White Pines in Forestation Programs

For use in forestation programs resistant parent trees are selected in accordance with Region 6 Tree Improvement Paper 53 and are grouped according to their level of resistance. These groups are recommended for use according to the white pine blister rust hazard classification of the forestation site. Refer to Table 7 for recommended use. These recommendations are based on currently available information and management of plantations to maintain good growth.

Table 7. Recommended Use of White Pines in Forestation Programs in Areas Where the Trees are Adapted.

Hazard*	Rust Index	Ribes/Acre	Stock Type	Max. Percentage of stocking
Very Low	<0.00005	<1	1. Seed from trees not selected for resistance.	100
Low	0.00005-0.005	1-25	1. Open pollinated seed from phenotypically selected trees for resistance.	25
			2. Open pollinated seed from genetically selected trees having reduced needle lesion frequency.	100
			3. Seed from seed production area, trees phenotypically selected for rust resistance.	100**
Medium	0.005-0.01	25-100	1. Open pollinated seed from genetically selected trees having reduced needle lesion frequency.	25
			2. Open pollinated seed from genetically selected trees having reduced needle lesion frequency and one or more other types of resistance.	50
			3. Seed from first generation seed orchards.	100
High	0.01-1.0	100-1,000	1. Seed from first generation seed orchards.	50
			2. Seed from second generation seed orchards.	100
Very High	1.0	>1,000	White pines. Plant alternate species.	0 100

* Hazard may be reduced by reducing the ribes population.

** May be reduced based on performance of composite sample of population in rust resistance evaluation at Dorena.

Definition of terms used in Table 5.

Hazard - The classification of an area according to the risk of infection of sugar pine and western white pine by white pine blister rust. Components of hazard classification include the following:

1. Susceptibility of white pines to white pine blister rust.
2. Susceptibility of ribes to white pine blister rust.
3. Virulence of local rust population.
4. Occurrence of climatic factors favorable for:

Ribes infection with aecia.
Intensification of rust on ribes.
Pine infection.

5. Land forms favorable for long distance spread of rust from ribes to white pines.

6. Stand structure as it affects rust spore dissemination from ribes to white pines.

Use the procedures developed by Regional Office Forest Pest Management to determine hazard.

Rust index - A numerical classification of hazard derived from Regional rust index program.

Ribes/Acre - The number of ribes plants per acre that are highly susceptible to white pine blister rust on the site. Ribes plants of lower susceptibility need to be identified in equivalents equal to highly susceptible ribes plants. This relationship needs to be locally developed for each distinct environment.

Stock type - Resistance in seedling population based on types and genetic control of resistant mechanisms in parents from which the population was derived. All parents shall be phenotypically desirable for other traits.

Maximum percentage - The maximum percentage of a particular stock type based on the hazard rating with reasonable expectation of adequate stocking.

J. Integrated Management in the White Pine: White Pine Blister Rust Host: Pest System

Resistance breeding is not the only procedure that can be used to reduce the impact of white pine blister rust on sugar pine and western white pine stands. Cultural procedures that maintain near optimum tree growth, branch canker pruning, and ribes eradication to reduce blister rust hazard are also viable ways to reduce the impact of white pine blister rust. In many areas, resistance plus one or more of these cultural procedures will give the best results.

Natural control of white pine blister rust is also a part of the Region's approach to the control of the rust. The older a blister rust canker the more likely it is to become inactivated or killed by a parasite (Hungerford 1977 and Kimmey 1969). The Region's multifactor line approach strongly keys in on resistance that reduces the rate of canker growth and thus allows more time for natural controls to become effective before a canker results in the death of a tree.

The multifactor line approach is considered to provide an additional level of horizontal resistance to the Region's white pine blister rust resistant sugar pine and western white pine program beyond that displayed in the multifactor lines. This is due to the multiline effect described by Nelson (1972) as follows, "Multilines exhibit horizontal resistance by curbing disease by reducing the amounts of effective inoculum of the right races at the right places." Advantage is also gained by maximizing resistant gene action effects (Nelson 1978) by randomizing individuals assigned to specific multifactor lines in seed orchards.

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